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THE BIOLOGY OF THE CRAYFISH

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INTRODUCTION

THE first reference to the crayfish in scientific literature is in Aristotle's "History of Animals," where he speaks of the "small Astaci which breed in the rivers." Aristotle and the older naturalists used the term Astaci to include both the crayfish and the lobster.

Faxon divides the crayfish into two great groups (24): One, restricted to the northern hemisphere, is found in Europe, Asia and North America. The other is found in the southern hemisphere, in Australia, Tasmania, New Zealand, Fiji Islands, Madagascar and South America.

The islands now inhabited by crayfish, such as England, Japan and Cuba, were probably once connected with the mainland.

In speaking of the distribution of the crayfishes, Faxon says:

> The northern family of crayfishes contains two genera, *Astacus* and *Cambarus*. These groups occupy distinct geographical areas. The genus *Astacus* is found in the old world in Europe and western Asia as far as the Aral and Caspian Seas, and in America in the region west of the Rocky Mountains, draining into the Great Salt Lake and the Pacific Ocean. It is thus seen to occupy the western sides of the two northern continents. *Cambarus* is found in North America east of the Rocky Mountains, in the region which is bounded on the north by Lake Winnipeg and New Brunswick, and on the south by Guatemala and Cuba. Crayfish thus are discontinuous genera, that is, genera which now occupy widely separated areas, such as *Astacus* in Europe and Pacific North America, but which once ranged over the intervening ranges as well.

It is comparatively easy to distinguish the common *Cambarus* from the *Astacus* of Europe and western America. Members of the genus *Astacus* have eighteen gills, while those of the genus *Cambarus* have but seventeen. The female of the genus *Cambarus* has a false pouch, the annulus ventralis, which serves as a sperm receptable, while in *Astacus* the sperm is deposited on the posterior part of the thorax in spermatophores.

Dr. A. E. Ortmann has made most careful studies of the distribution of the crayfish. References to his papers will be found in my bibliography. Dr. Ortmann writes me that there are in the United States and Central America, 74 species of *Cambarus* and 5 of *Potambius* (*Astacus*). In the United States excluding Mexico, Guatemala and Cuba, there are 64 species of *Cambarus* and 5 of *Potambius*.

The European word "crayfish" is used by teachers of zoology, probably because of Huxley's classic, "The Crayfish."

Ortmann found (38) that not only was "crawfish" used by Say, 1817, earlier than "crayfish" by Huxley, 1880, but that in this country "crawfish" is the popular name.

"Crayfish," "crawfish," or, as it is sometimes incorrectly called, "crab," come from the same root, Old German, "Krebis," from which are derived, on the one hand, the modern German " Krebs " and the English " crab "; on the other hand the French " ecrevisse," the English and the American " crayfish."

The crayfish on which my own observations have been centered belong to the species *Cambarus bartonius bartoni,* the only species which has migrated into New England.

My work was carried on in the field and in the laboratory continuously for nine months. In the field I have watched the activities of the crayfish in the small ponds with which Worcester, Mass., is so well supplied. At night I used a powerful acetylene gas lamp. In the laboratory I made use of two large aquaria, one of them an ordinary running water aquarium with a pile of sand at one end, and the other a still water aquarium arranged to furnish a more nearly natural habitat.

In this paper I have not touched upon the anatomy or the work on regeneration, but have confined myself to what is generally known as ecology or biology. In the attempt to make the paper fairly complete I have referred in the text to the numbers in the bibliography.

It is a pleasure to acknowledge my indebtedness to Dr. C. F. Hodge, Dr. Newton Miller and Dr. J. P. Porter, of Clark University, Dr. A. E. Ortmann, of the Carnegie Museum of Pittsburgh, and Dr. E. A. Andrews, of Johns Hopkins University.

SENSES

Touch.—Touch is probably the sense of greatest value to the crayfish. It is sensitive to touch over the whole surface of the body (16), especially on the chelae and chelipeds, mouth parts, the ventral surface of the abdomen and the edge of the telson.

Vision.—The crayfish, in common with the insects, has a compound eye. It is believed by many that the compound eye is a visual apparatus which is almost worthless for detecting the forms of objects, especially if these objects are stationary; but that it may furnish a very definite response to stimuli of moving objects.

Bell's experiments with the crayfish (16) showed that there was no response to stationary objects. The case was entirely different with large, moving objects. The response was not due to any change in the intensity of light such as that caused by a shadow falling on the animals, for they would react to a movement made on the opposite side of them from the window. Reaction to smaller moving objects was not so marked.

Crayfish are sensitive to strong light and hide during the day under stones, among roots of plants near the bank, and in burrows in the bank. It is a noteworthy fact that, in France, the people catch crayfish by building huge fires on the bank at night to attract them.

My own experiments indicate that in nature the crayfish will retreat from a strong light, but will approach a dim one. In the spring I found that it was extremely difficult to frighten a crayfish from its food by means of my acetylene light. In collecting at night it is very easy to attract crayfish from some distance by setting a light on the bank so that it dimly illuminates some little space of water.

Smell and Taste.—Very little experimental work to determine the senses of smell and taste in any of the crustacea was done until Bell, in 1906, tested the reactions of the crayfish (15) to chemical stimuli, applying meat juice by means of a fine pointed pipette to various parts of the body. He found that the antennæ, antennules, mouth parts and chelipeds were especially sensitive.

Recently (1910) Holmes and Homuth published the results of an extended series of experiments on crayfish in which the outer or inner rami of the antennules were removed; the antennules were removed entirely; the antennæ were removed; the chelipeds removed; and in some specimens the brains were destroyed (33).

They found that the outer rami of the antennules bearing the olfactory setæ were especially sensitive to olfactory stimuli, that the inner rami of the antennules, the antennæ, the mouth parts and the tips of the chelipeds were all sensitive to some extent to olfactory stimuli.

It is probable that in the crayfish we have a very highly developed topochemical sense, or contact-odor sense. Forel uses this term (25) in speaking of the fact that in ants, odors are apparently detected by the contact of the antennæ.

Bell found that the crayfish was sensitive to food when *not* in contact with it. I experimented with freshly cut meat and with meat which had been exposed to the air for some time so that the cut surfaces had dried, and found that the crayfish would go toward and seize the fresh meat first. Evidently the diffusion of the meat juices was readily detected.

Hearing.—It has been pretty clearly demonstrated by Bell that the crayfish has no sound reactions. He tried experiments (16) such as rapping on a board floating in the water, snapping a metal snapper in and out of the water, and setting tuning forks in vibration in the water, but got no response.

It is possible that the crayfish is sensitive to the sound made by the movement of the *mouth parts* of another crayfish. This has not been proved.

Equilibrium.—Bunting found that young crayfish with the statocysts removed would swim upside down as readily as right side up (18). It is also pretty certain that the older crayfish have a sense of equilibrium, although the response to rotation in their case is not definite, but purely individual.

MATING, SPAWNING AND DEVELOPMENT.

The process of mating in *Astacus* differs from the process in *Cambarus*. In the case of *Astacus,* the males approach the females in October, November and January.

> The male seizes the female with his pincers, throws her on her back and deposits the spermatic matter, firstly on the external plates of the caudal fin, secondly on the thoracic sterna around the external openings of the oviducts. During this operation the appendages of the first two abdominal somites are carried backwards, the extremities of the posterior pair are enclosed in the groove of the anterior pair; and the end of the vas deferens becoming everted and prominent, the seminal matter is poured out and runs slowly along the groove of the anterior appendage to its destination, where it hardens and assumes a vermicular aspect (20).
>
> After an interval of from ten to forty-five days, oviposition takes place. The female rests on her back and bends the abdomen forward, forming a chamber into which the oviducts open. The eggs are passed into the chamber by one operation, usually during the night, and are plunged into a viscid, gray mucus with which it is filled. The spermatozoa pass out of the spermatophores and mix with this fluid, fertilizing the ova, but just how, and what becomes of them, are unknown (20).

The female of *Cambarus* differs from the female of *Astacus* in having a false pouch, the annulus ventralis. Andrews found that this pouch does not appear in *Cam-*

barus affinis until the individual has reached a third stage after leaving the egg.

The method of sperm transfer in *C. affinis,* and that of *C. b. b.* as well, is as follows:

> The male everts the bent, nozzle-like papillæ at the mouth of the vasa deferentia and through them discharges sperm into an actual tube that passes down each of the first two abdominal appendages or stylets. Both first and second pairs of stylets are locked together by a peg and groove contrivance. The sperm thus passes through a closed tube from the vasa deferentia into the annulus ventralis without coming into contact with the water. Copulation lasts from two to ten hours and may be repeated by either animal with some other (3, 4).

In a previous paper, I pointed out (21) that the males do not distinguish the females and that males "repeatedly grasp other males, and sometimes, in spite of their frantic struggles turn them over and attempt to copulate with them." The crayfish is at such a state of nervous tension during the period of sexual activity, that the female will curl her abdomen at the slightest touch and the male will at first grasp any rounded object presented to him and attempt to overturn it. A stimulus so slight as the slow lowering of the water when I siphoned it from the closed tank, was sufficient to cause violent activity among the males, with the result that all the females were soon held by males.

Pearse, in a study of crayfish made in the laboratory with no attempt to reproduce natural conditions (40), has made many interesting observations and experiments, verifying my statements (21) and adding the discovery that a male will copulate with a dead female. He discovered that the male of one species had succeeded in adjusting his stylets to the annulus of a dead female of another species.

Andrews has just published a paper (13) in which he mentions seeing males attempt to copulate with dead and bound or paralyzed males and to actually go through all the activities of mating with dead females except the injection of the spermatophores and plugging of the annulus. He agrees with my previous statement that the males do not recognize the females, and suggests that the difference from the standpoint of the crayfish between the sexes is a difference of behavior, which difference is perceived by muscle and touch sense.

The passivity of the female when seized is marked in the crayfish, but as I shall show in another paper, in the marine crabs the female is not passive but aids in the movements preliminary to conjugation.

It is possible, though I have not at present enough observations to support the theory, that in the crayfish and the lobster, deposition of sperm is most effective when the female has just moulted and the annulus ventralis or the ventral surface, as the case may be, is clean. In crabs where fertilization is internal, it is necessary that the shell be soft; softness is of course of no use where the fertilization is external, in fact it might be injurious; but the cleanness of a new coat may facilitate the deposition of the spermatophores, and the retention of the plug.

Anatomically there should be no difficulty in crossing the different species of *Cambarus*. It would be interesting to see if spermatophores deposited by a male *Astacus* on the shell of a female *Cambarus* would fertilize the eggs. It is quite probable, however, that the female would not leave the spermatophores on her thorax and abdomen until the time of egg extrusion.

Andrews (13) transplanted sperm receptacles of several females to females of another species and the mutilated females lived to lay eggs but the eggs did not develop. Males would not fill the transplanted receptacles. Andrews found that conjugation between species may take place to some extent, but did not succeed in any case in securing sperm transfer and actual crossing of species.

There seems to be no well-marked mating season in the cold-water species, including the species on which my observations were made. In the ponds, mating crayfish were not found later than November 1, but in the laboratory copulation occurred at intervals during the fall, winter and spring. It is probable that in its native haunts the crayfish behaves differently.

In the spring the males die off in great numbers. This is a phenomenon which is noted in many arthropods, and seems to be a wise provision of nature to prevent the now useless males from using up the food required for the spawning females and the young crayfish. Some of the males, however, live to a good old age. I have found several that were over 90 mm. long.

In the case of *C. bartonius bartoni* there are two more or less well-marked spawning seasons, fall and spring.

The fall laying, as indicated by females brought into the laboratory, is during the latter part of September and all through October and November. The spring laying extends from about March 15 to about May 15.

Andrews observed the process of laying in *Cambarus affinis*. For four or five days previous to laying, the female cleans her abdomen diligently and is exceedingly sensitive to disturbances during that time. The actual laying is done in deep water at night. It takes from ten to thirty minutes to extrude the two hundred to four hundred eggs. Each egg is attached by a tiny filament to the abdominal hairs (9).

The time of fertilization is supposed to be when the eggs are laid, as they pass over the annulus ventralis. Andrews found that on the removal of the annulus before the eggs were extruded, the eggs were unfertilized and did not develop.

When first extruded the eggs are almost black, but as development goes on they become reddish in color and at the end of about four weeks, when the young crayfish are hatched, they are nearly transparent. The time of development, from the extrusion of the eggs till the crayfish are detached from the parent, is about eight weeks in the species which I studied.

Even after the young are detached from the swimmerets of the mother, for several days they do not venture far from her, and taking warning at any apparent danger, scuttle under her abdomen. It is probable that here the visual sensitivity to moving objects is more highly developed than in the adult in comparison with other senses.

The young crayfish moults very frequently during the first year.

I found that two or three days before moulting the adult crayfish come up into the shallows exposing their carapaces and drying them out thoroughly. The first time that I saw this prolonged drying-out process I did not think it significant, for I have seen crayfish in ponds where the water was pure and fresh, elevating their carapaces for a few minutes at a time. It is a habit which is not necessarily caused by impure water, for the same thing was noted by me in the laboratory with animals in the running-water tank.

When I noted by the number (in oil paint) on its back that the same individual was continually remaining only partly submerged, I made a note and watched developments. Later, in three other crayfish I noted this preliminary drying out, and predicted the approximate time of the moults. This was convenient knowledge, for a crayfish in difficulty with his half removed old coat falls easy prey to his brethren.

It is possible that the aeration of the attached young by the mother is for the purpose of enabling the young crayfish to moult more readily. Observations like these have not been reported for other crayfish or for marine crustaceans, but it seems possible that in the crayfish we have such a drying out of the old exo-skeleton as we find taking place in insects, like the dragon fly, which live for a time in the water.

Andrews made a thorough study of the young of both *Astacus* and *Cambarus* and found that in *Cambarus* the young four months old averaged about 41 mm. in length. During the winter of the first year there is no increase in size, but the second summer of life marks an increase of thirty per cent. in length (12).

I have found females but one year old with eggs, and the development went on in the laboratory just as in the more mature females. The largest female that I captured was 102 mm. in length. The largest male was 90.5 mm. long.

Food.

Crayfish are omnivorous. I have previously shown that *C. bartonius bartoni* prefers fresh animal food to stale animal food or either fresh or stale vegetable food (21).

Some crayfish eat a great deal of vegetable matter, one species, the chimney builder, *Cambarus diogenes,* seeming to prefer it. The vegetable matter eaten consists of dead leaves, potato, onion, young corn and buckwheat.

The animal food consumed by the crayfish consists of worms, insects, insect larvæ, a few fish, frog, toad and salamander eggs, and occasionally a dead fish or frog. I have seen crayfish devour a hapless relative who was endeavoring to rid himself of his old shell. Sometimes females eat eggs from their own abdomens and even devour their own freed offspring.

Enemies.—The crayfish suffers from internal and external enemies. Among the plants which live symbiotically with the crayfish are diatoms, bacteria and saprolegnia. Internally, *Distoma cerrigerum* and *Branchiobdella* have been noted. But these are not all the enemies of the crayfish. Besides man, who uses thousands of dollars worth of crayfish for food and as a garnish, many small animals find them palatable.

Many fish, including the black bass, *Micropterus,* which fishermen find very partial to crayfish, eat them.

Professor Surface reported (38) that the salamanders *Cryptobranchus allegheniensis* and *Necturus maculosus,* are among the chief enemies of the crayfish.

Ortmann mentions seeing the water snakes, *Natrix sipedon* and *N. lebens,* when captured, disgorge crayfish and has also found garter snakes, *Eutænia sirtalis,* in the holes of *Cambarus monongalensis.*

In the laboratory and in the field I have found that the common box turtle catches many crayfish.

Many birds, including the eagle, king-fisher, wild ibis and turkey, have been observed with crayfish in their claws; or the remains have been seen at the nests.

CRAYFISH AS INJURIOUS CREATURES.

The river species do not especially injure human interests except in occasionally capturing a few toads, fish and frogs, but the burrowing species are cited by Ortmann (38) as being very injurious, especially in the lowlands of Pennsylvania, Maryland and West Virginia.

They make mud piles which clog harvesting machines, and are considered by the farmers in Maryland as such pests that it is common to throw unslacked lime over the fields in order to kill the unwelcome tenants.

West Virginia farmers claim that the crayfish destroy crops of buckwheat, corn and beans by eating the young sprouts.

Great damage is done by the burrowing species *Cambarus diogenes,* in burrowing into dams on ponds and reservoirs, one notable instance being the levees of the Mississippi (38).

To destroy crayfish it is customary to throw unslacked lime over the fields, or to pour carbon bisulphide into the holes, or to drain the infested area.

None of these measures is efficacious, the first two methods being impracticable on account of the difficulty in reaching the bottom of the burrow and the second, simply lowering the water level, only delays matters a little.

VALUE OF THE CRAYFISH.

At the present time, with the lobster fishery in a state of decline, it seems as if the crayfish could be profitably substituted for its larger cousin.

In a carefully written paper (11) Andrews sets forth the possibilities of crayfish propagation.

He states that, from the small region on the Potomac between Washington and Fort Washington, it was estimated that there were half a million crayfish sent annually to New York.

New York, New Orleans, Chicago, Milwaukee and San Francisco, and many other large cities consume large quantities as food.

In 1902, the U. S. Fish Commission reports state the crayfish catch of Monroe Co., Florida, was 55,664 pounds, worth $3,382.

In Oregon, 116,400 pounds, worth $7,760, were caught in one year.

With crayfish maturing in one season and growing to a length of from four to five inches in three years; and considering the large number of eggs (100–600) laid by one female, there should be but little difficulty in supplying a large demand for these animals.

When we consider that the large *Astacus* readily adapts itself to the slight difference in environment in the east, we see that the crayfish is a very practicable substitute for the lobster.

There should be no difficulty in disposing of the smaller *Cambarus,* either as fresh food or canned, as we get the abdomens of shrimps.

In the school and college laboratories, the anatomy of the crayfish has been studied ever since Huxley wrote "The Crayfish." The habits and activities of the young and adult crayfish are of great interest and profit for study. The animal is suited for many kinds of experiments, and the large ganglia and nerve cells are readily removed and are excellent for neurological work. The psychologists should find a profitable subject for study in the relations of mother and offspring for the few days just after the young are detached from the mother's swimmerets.

Daily Life.—From a lengthy series of observations, including the continuous study of several specimens for twenty-four hours, I have concluded (21) that the crayfish shows his greatest activity at nightfall and at daybreak. In nature the crayfish is less active during the day than he is in captivity, since, as a rule, he has more hiding places in his natural habitat.

Pearse has stated (40) that the number of matings occurring in two boxes, one being painted black and closed entirely, and the other being exposed to light, did not vary to any extent. It is obvious from the work of Andrews and myself that the fact that crayfish in a state of sexual tension, stimulated by transference to different receptacles, copulate as well in the light as in the dark, does not bear on the question of normal activity. The difference between night and day must not be assumed to be entirely that of light, in experiments on higher invertebrates.

It is possible that the tendency of the crayfish to remain in hiding during the day is to some extent lessened when sexual feeling is strong, but this seems rather improbable under natural conditions.

In my specimens hibernation was well marked. I was careful to change the water daily in my still-water aquarium, thus keeping it fairly cool. Several of my crayfish hibernated as long as six weeks at a time, in closed burrows in the bank of this miniature pond.

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